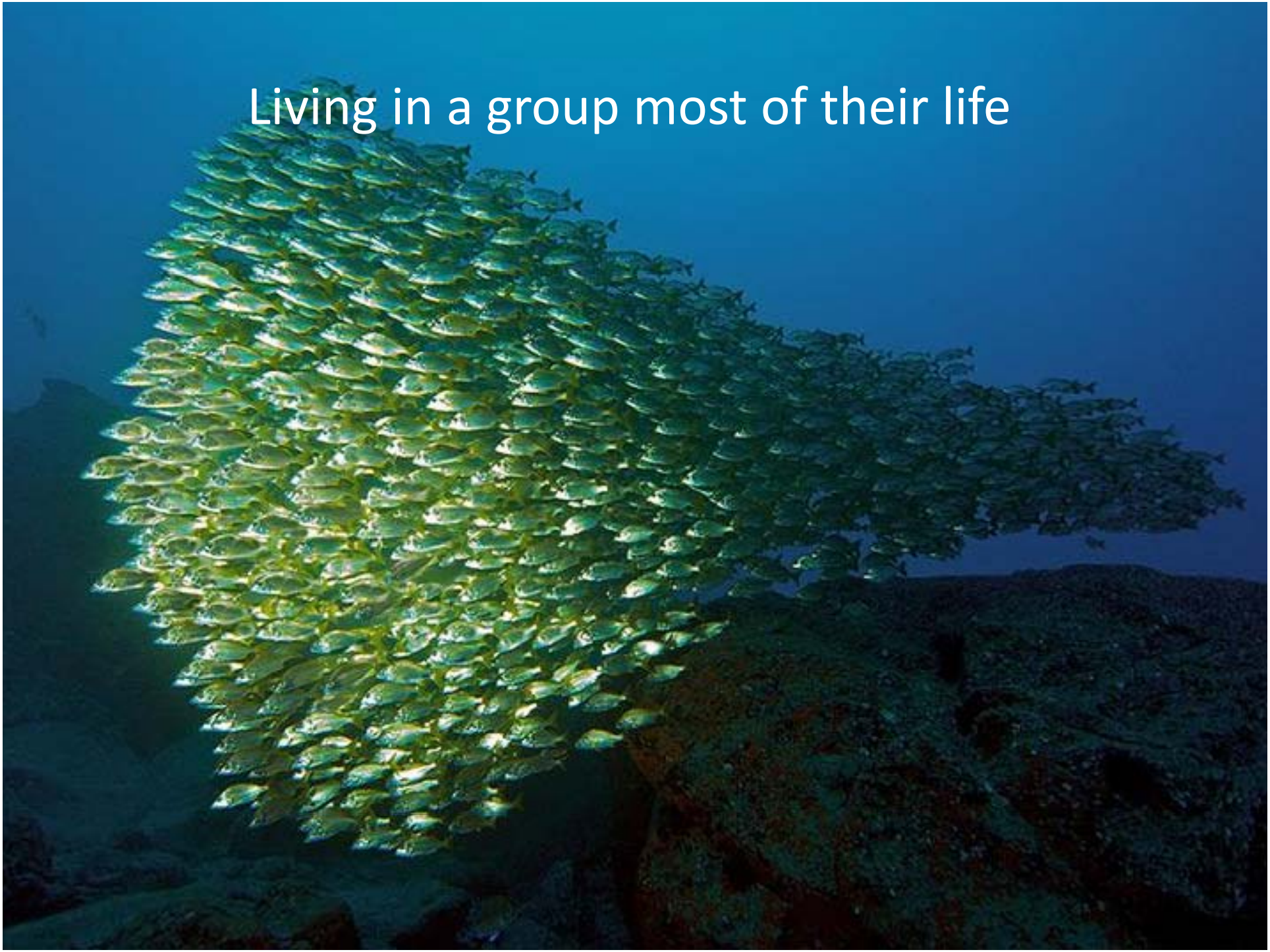
Evolution of social behavior

Social behavior:

Inter-individual relationships among the members of that population.

- solitary, pair-bond, family, colonial, aggregation/ schooling


Living in a group most of their life

Some species are more social than others?

Some species are more solitary than others?

Why ?(ultimate causes)

More social means more adaptive?

More social means more adaptive?
No, not really.

Natural selection assumes that behaviors evolved to best adaptive to species-specific environment. Solitary behavior could be more adaptive if this behavior provides more reproductive success.

Social or solitary life is both adaptive

depending on

benefits and costs of social life of each species

Costs of social living

1. Conspicuousness to predators
2. Greater transmission of disease and parasites
3. More competition among group members
4. Male vulnerability to cuckoldry
5. Female vulnerability to egg dumping, tossing
6. Expend time/energy jockeying for social status

The costs of social life

Pathogens (virus) affect colonial free-tailed bats

The costs of social life

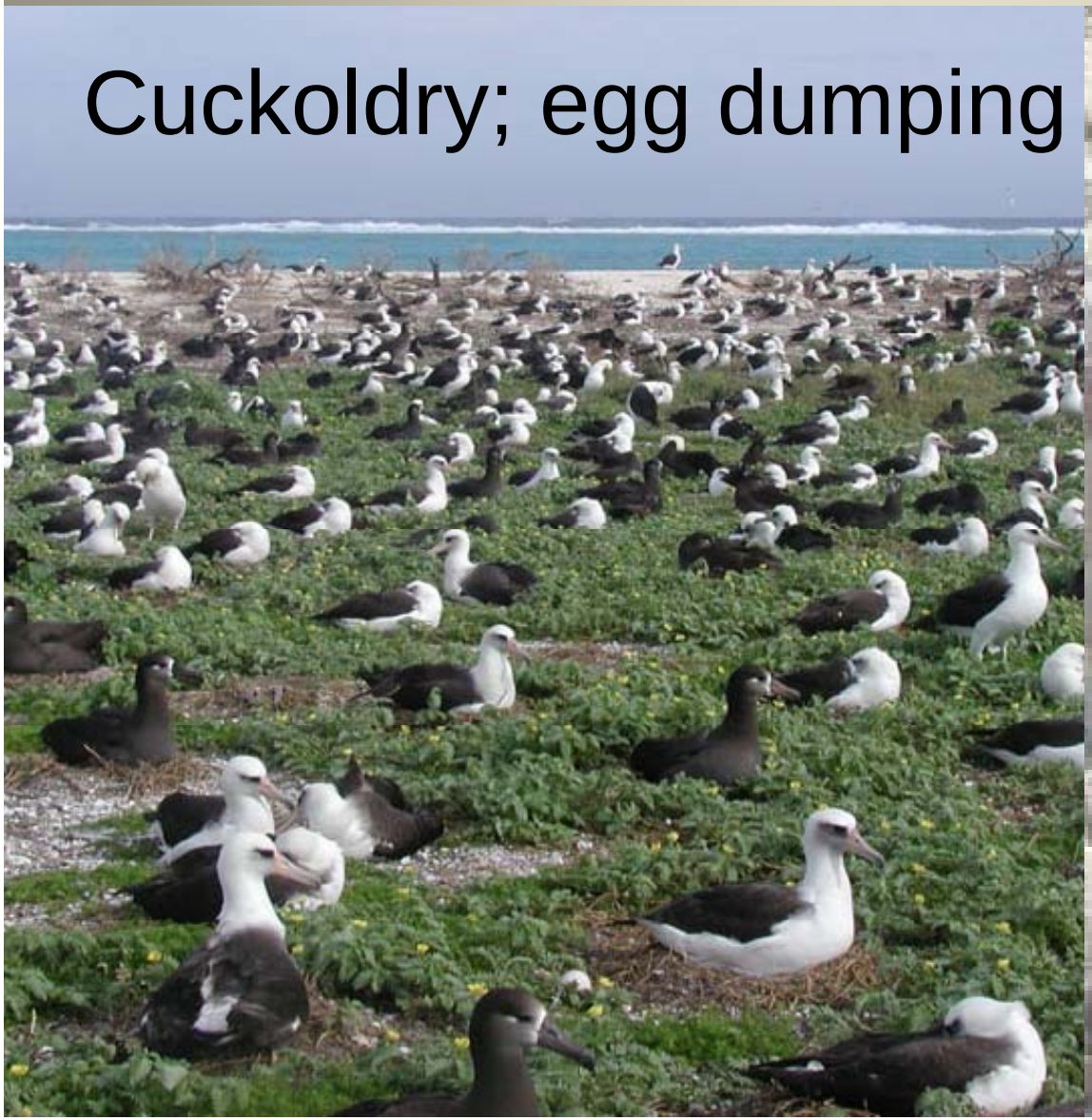
Effect of parasites (bugs) on cliff swallow nestlings

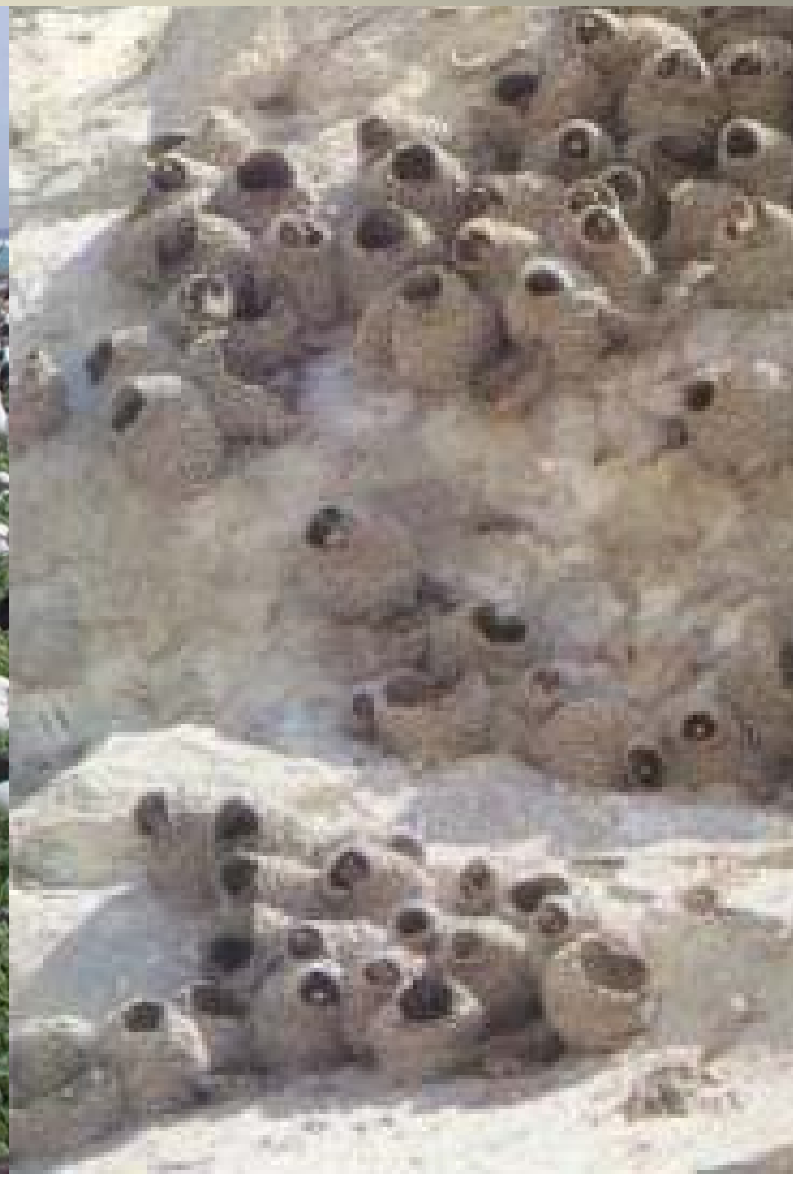
Which nestling (same age) suffers from parasite infection?

Parasites (fly larvae) in nestling birds

The costs of social life

Cuckoldry; egg dumping



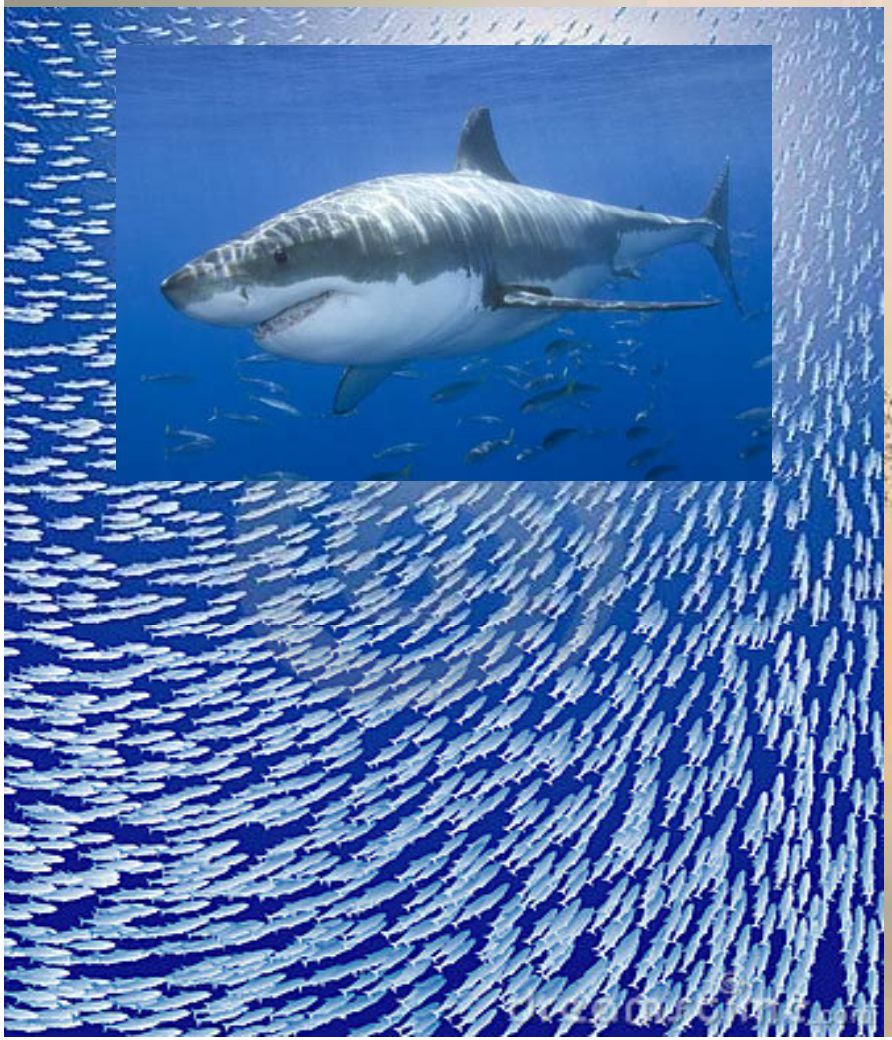


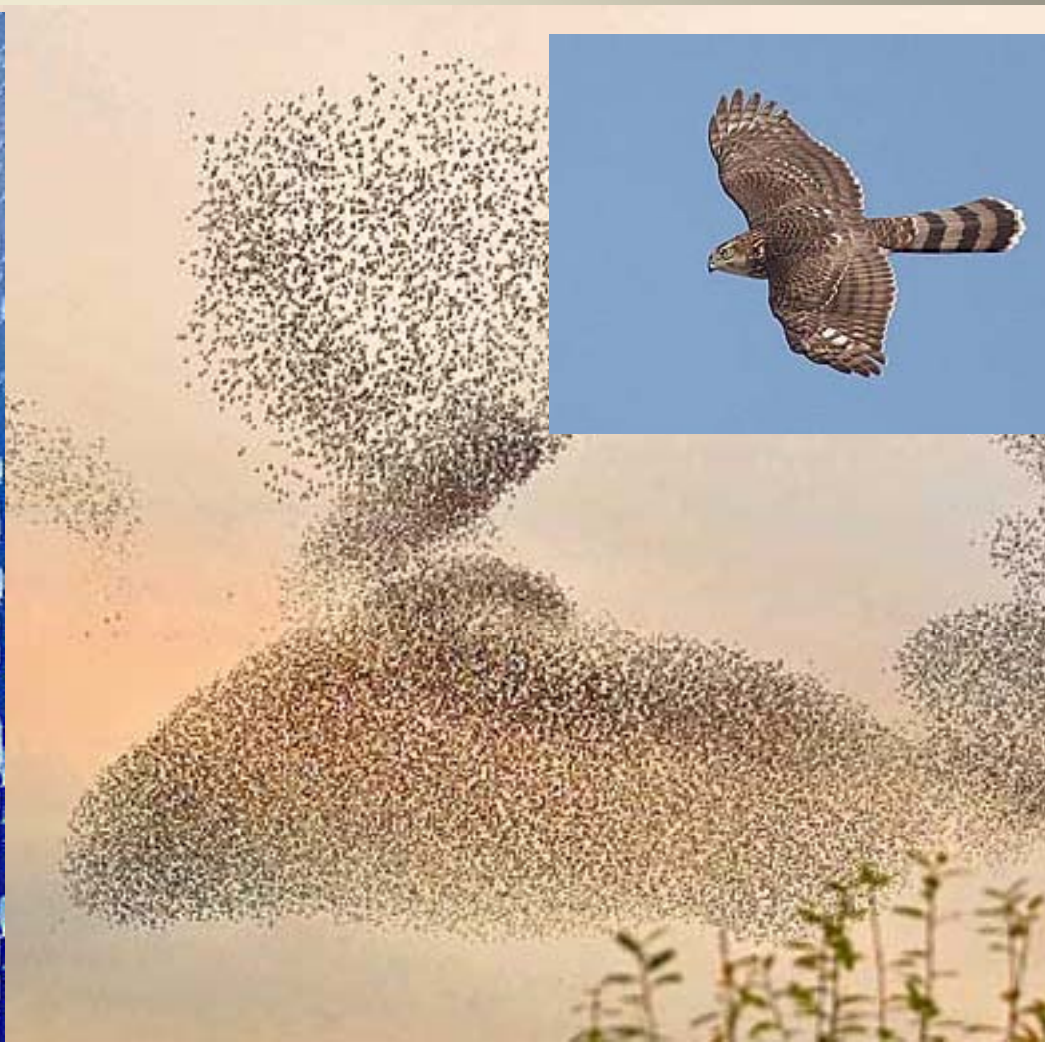
Benefits of social living

1. Group defense against predators
2. Acquire information of food resource from others
3. High/ low social status benefits
4. Chance for cuckoldry
5. Opportunities for egg dumping, tossing

The benefits of social life

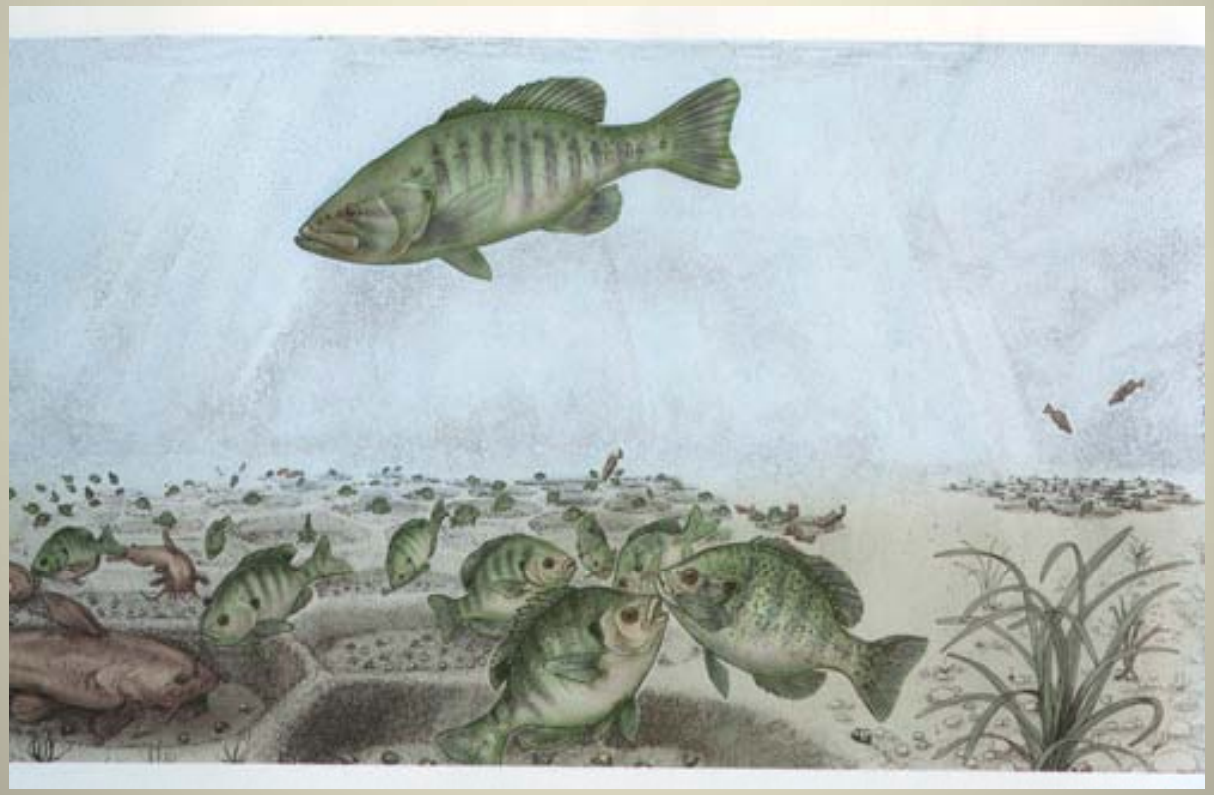
Group defense: 1. dilution effect



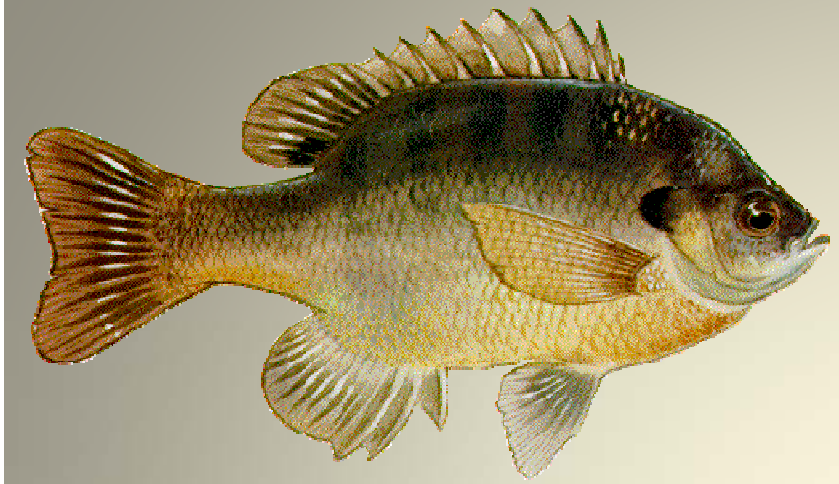


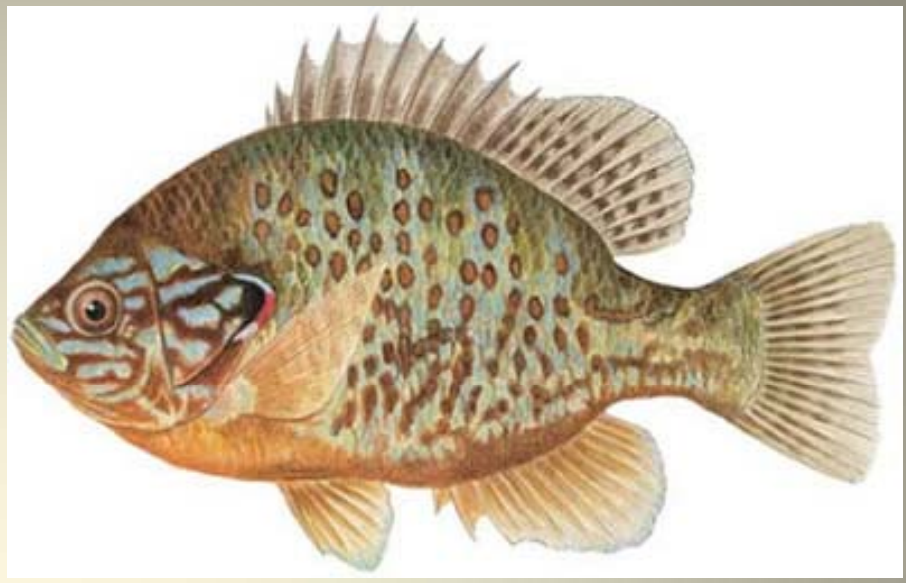
The benefits of social life

Group defense: 2. mutual defense



Bluegills defend egg-eating predators





Bluegills
Colonial

Pumpkin sunfish
close-relatives of bluegills
Solitary ;

Solitary sunfish has powerful biting jaws and
So can repel egg-eating enemies on its own;
It does not need social life for defense

The evolution of helpful (social) behavior

Helpful behavior

How does it evolve
through natural selection?
(benefit > cost)

Natural selection select for
Gene / Individual / Group??

Until mid-1960s, biologists took helpful behavior for granted because they assumed that animals should assist one another for the benefit of the species as a whole (one should help each other)

Group selection ?

But, does group selection work?

Lemmings (rodents)

Extreme population fluctuation

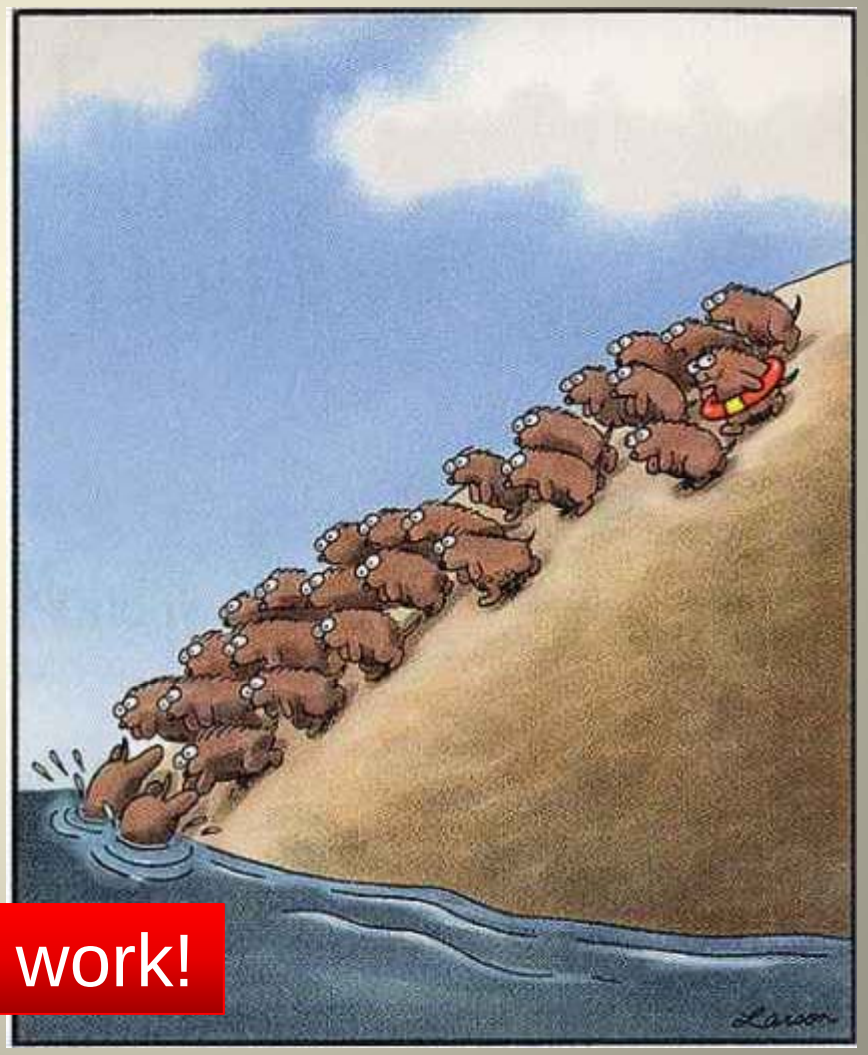
High population density →

→ Dispersal → many died

→ commit suicide (?) to control population size, for the benefit of lemming species?

Cheaters will have reproductive success, and their “cheating” genes will prevail!

Lemmings (rodents)



Group selection doesn’t work!

The gene as the unit of selection?

Selfish gene theory

Differences in genes give rise to differences in these phenotypic effects. Natural selection acts on the phenotypic differences (e.g., behavior..) and thereby on genes. Thus genes come to be represented in successive generations in proportion to the selective value of their phenotypic effects.

….genes build vehicles to promote their mutual interests of jumping into the next generation of vehicles…. organisms are the survival machine of genes. (organism as vehicles)

Types of social interactions

1. Mutualism (cooperation)
2. Reciprocal altruism
3. Altruism
4. Selfish behavior
5. Spiteful behavior

1. Mutualism

Helper (gain); recipient (gain)

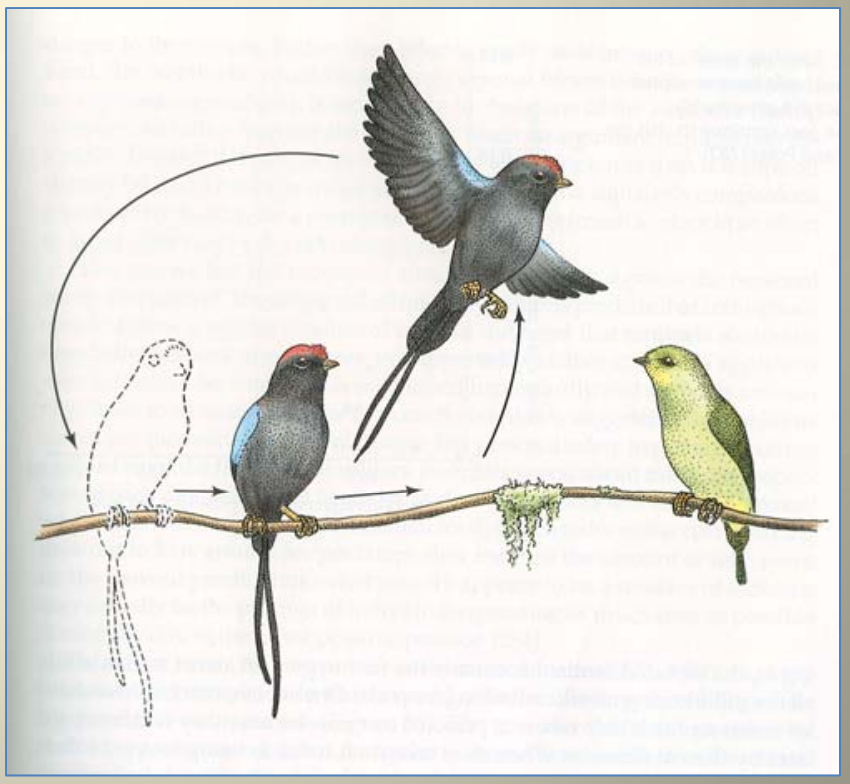
Both helper and recipient have reproductive gains from their interaction.

Examples?


Cooperative courtship of
the long-tailed manakin

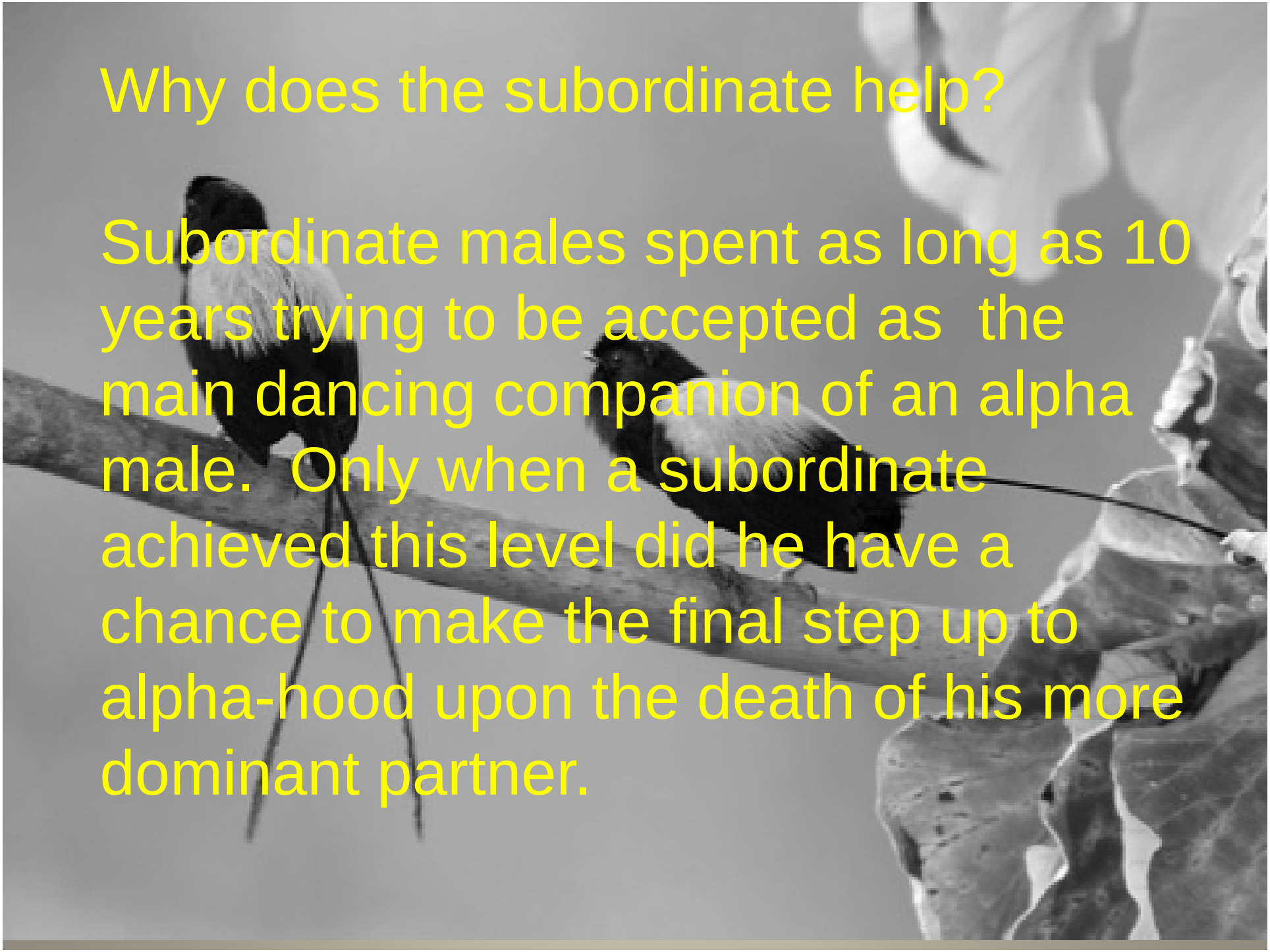
Cooperative courtship of the long-tailed manakin

One is dominant, the other is subordinate.



Why does the subordinate help?

--increase the mating chance



Why does the subordinate help?

Subordinate males spent as long as 10 years trying to be accepted as the main dancing companion of an alpha male. Only when a subordinate achieved this level did he have a chance to make the final step up to alpha-hood upon the death of his more dominant partner.

Types of social interactions

1. Mutualism (cooperation)
2. Reciprocity
3. Altruism
4. Selfish behavior
5. Spiteful behavior

2. Reciprocity

Helper (gain-delayed); recipient (gain)

Both helper and recipient have reproductive gains from their interaction, but helper's gain will be delayed.

2. Reciprocity

Social grooming

2. Reciprocity

-- Game theory --

Methods of studying strategic decision making.

An animal's behavior is based on the other's action.

Example #1 hawk/ dove game

Example #2 prisoner's dilemma

Game theory- hawk/ dove game

Player 1 (animal 1)

Player 2 (animal 2)

	Hawk	Dove
Hawk	$(v - c)/2$	v
Dove	0	$v / 2$

Decision making is based on the benefits and costs of the action and its consequence

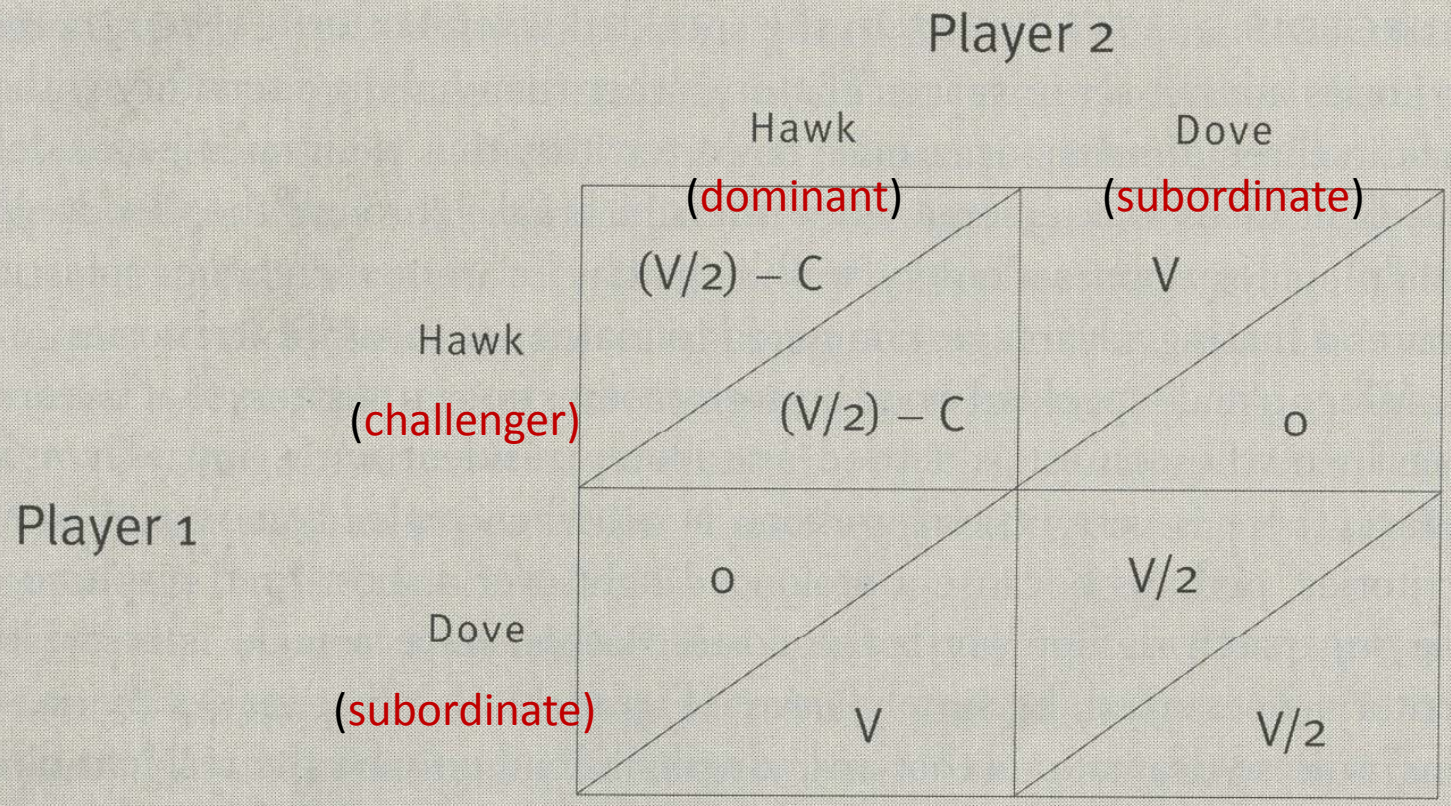
Game theory

1. The hawk-dove game

Example: Social dominance hierarchy

Hawk-Dove game in a social group

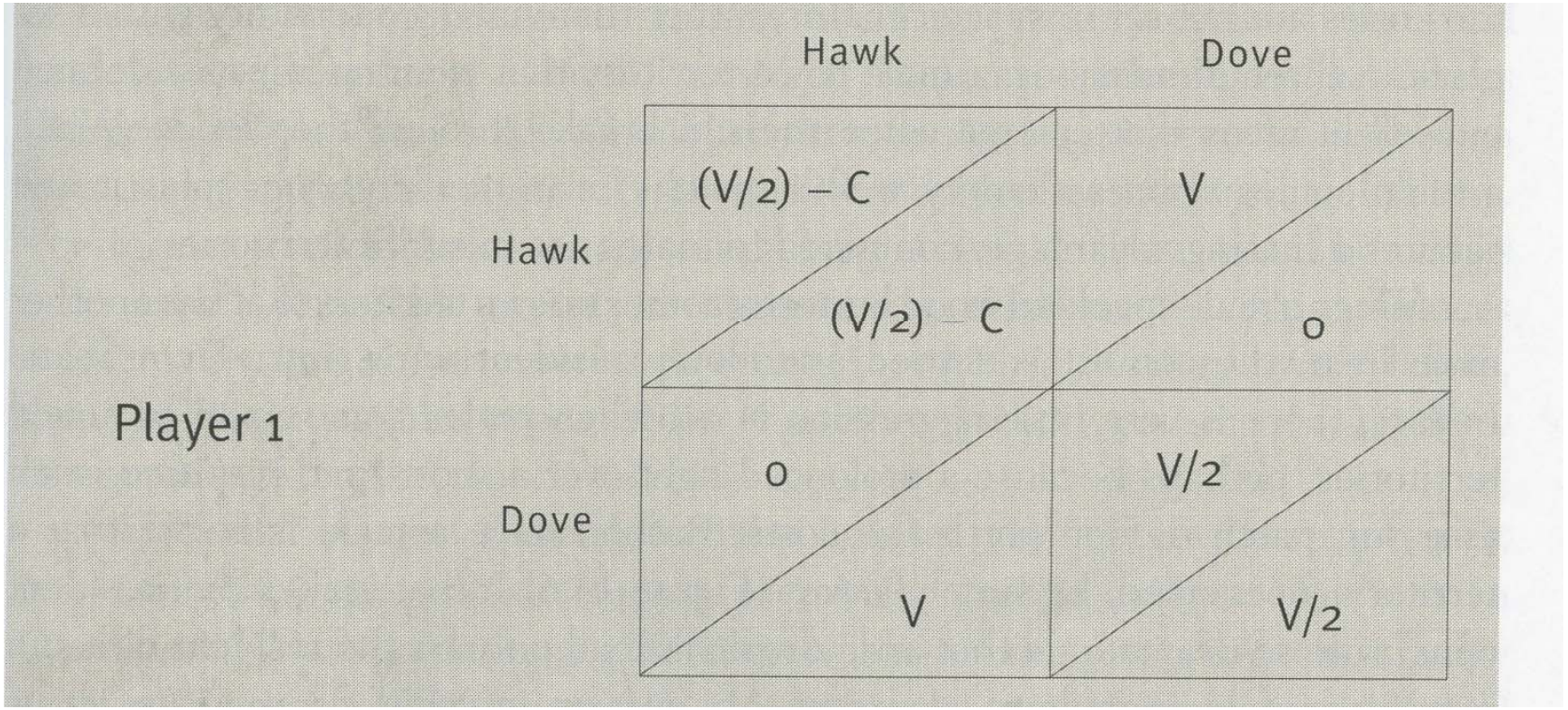
TABLE 14.2. The payoff matrix for the hawk-dove game. Both player 1 and player 2 choose between the hawk (always be aggressive) strategy and the dove (bluff, but retreat if opponent escalates) strategy. V = value of resource, C = cost of fighting. Payoffs to Player 1 are shown above the dashed line, and payoffs to Player 2 are shown below the dashed line.



If V> C, then Hawk is an evolutionary stable strategy:

V/2-C >0;

V/2<C (not as good as to be a dove)



Bourgeois strategy

Individual to play hawk if it is a territory holder

Individual to play dove if it does not own a territory

Bourgeois strategy (Speckled wood butterfly)

M1 (experimentally made a territory owner) always defeated an intruder male, M2.

If M1 was removed from his territory, M2 occupied it for a while, M1 would now defer to M2

Social dominance hierarchy and its costs (stress)

Short term stress of social dominance hierarchy

During fight-or-flight response (short term stress response):

1. Adrenaline and norepinephrine surge in blood sugar, and oxygen are delivered to the brain, muscles, and heart

2. Non-essential systems, digestive and reproductive system, temporarily shut down

3. Evaluate the costs and benefits of fighting.

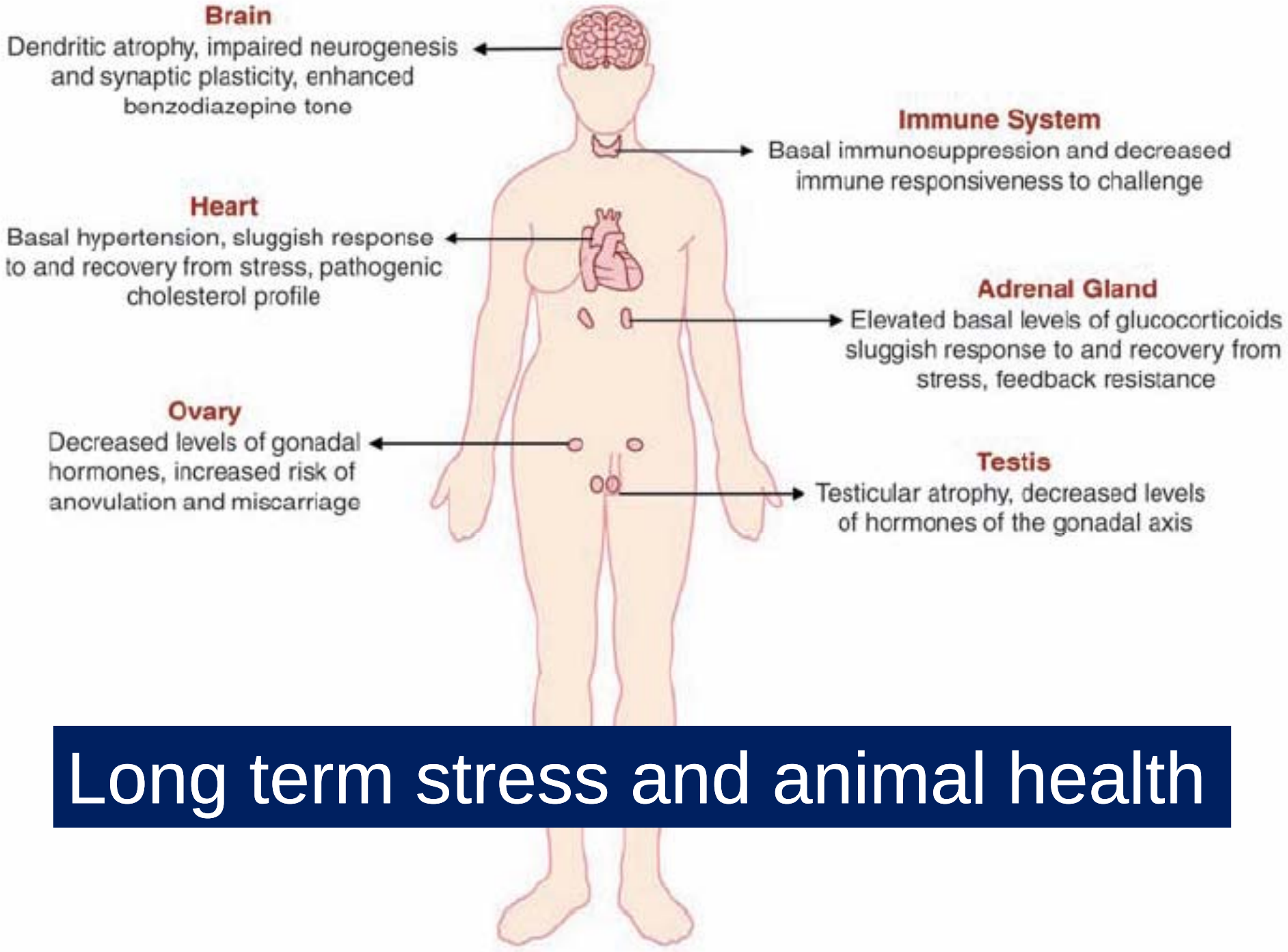
Long term effect of dominance hierarchy

Stressful social ranks

Higher levels of stress hormones (GC)

Lower immune system against pathogens

Reduced number of synapses;
Reduced number of neurogenesis;
Physical/ mental health deterioate…



Long term stress and animal health

It is not easy to be the dominant one…

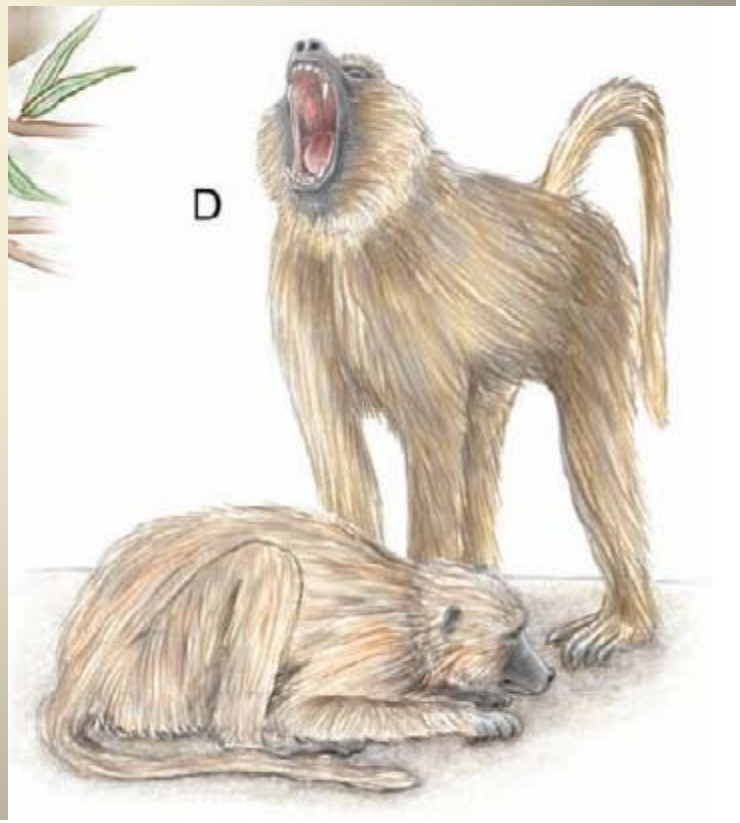
Highly stressful, particularly if

1. Hierarchy is not stable, frequently challenged by others.
2. Dominance through fight, intimidation.
3. Resource inequity (more intense competition for resource)
4. Breeding cycles.

It is not easy to be the subordinate…

Highly stressful if…

1. In a stable hierarchy
2. In male-dominant social hierarchy
3. Less resource inequity



Subordinates cope with stress…

Social support
(grooming, coalition…)

Game theory

2. Prisoner’s dilemma

Game theory: Prisoners' dilemma:

Two men are arrested, but the police do not possess enough information for a conviction. Following the separation of the two men, the police offer both a similar deal—if one testifies against his partner (defects/betrays), and the other remains silent (cooperates/assists), the betrayer goes free and the cooperator receives the full one-year sentence. If both remain silent, both are sentenced to only one month in jail for a minor charge. If each 'rats out' the other, each receives a three-month sentence. Each prisoner must choose either to betray or remain silent; the decision of each is kept quiet. What should they do?

2. Reciprocity-prisoners' dilemma

		Player B	
		Cooperate	Defect
Player A	Cooperate	Reward for mutual cooperation	Maximum punishment
	Defect	Maximum reward	Punishment for Mutual defection

Prisoner's dilemma

Payoffs for player's response ranks….

1. Defect while other players cooperate
2. Both cooperate
3. Both defect
4. Cooperate while other player defects

Optimal response: always defect, never cooperate.
if it is one-time game and playing with a stranger

1. play one time only with a stranger….
   *what strategy will you gain most?

2. play 10 times with someone you know…
   *what strategy will you gain most

"The Prisoner's Dilemma"		Individual #2	
		Cooperate	Defect
Individual #1	Cooperate	(3,3)	(0,5)
	Defect	(5,0)	(1,1)

Reciprocity might not work for one-time game playing with a stranger….

However, it works if two players interact repeatedly.

For reciprocal altruism to work as a strategy, several conditions are required:

1. Frequent interaction (play >1 game)
2. Recognizing individuals
3. Remembering past interactions with individuals
4. Assisting only those who provided past assistance

“ tit for tat” strategy

(reciprocity strategy based on prisoner’s dilemma)

Tit for tat strategy

An individual cooperates on the initial encounter with a partner subsequently copies its partner's pervious move.

1. If the partner cooperates, then cooperate.
2. If the partner defects, then defects.

Tit for tat strategy

Three fundamental characteristics

(1) Nice: never cheats first

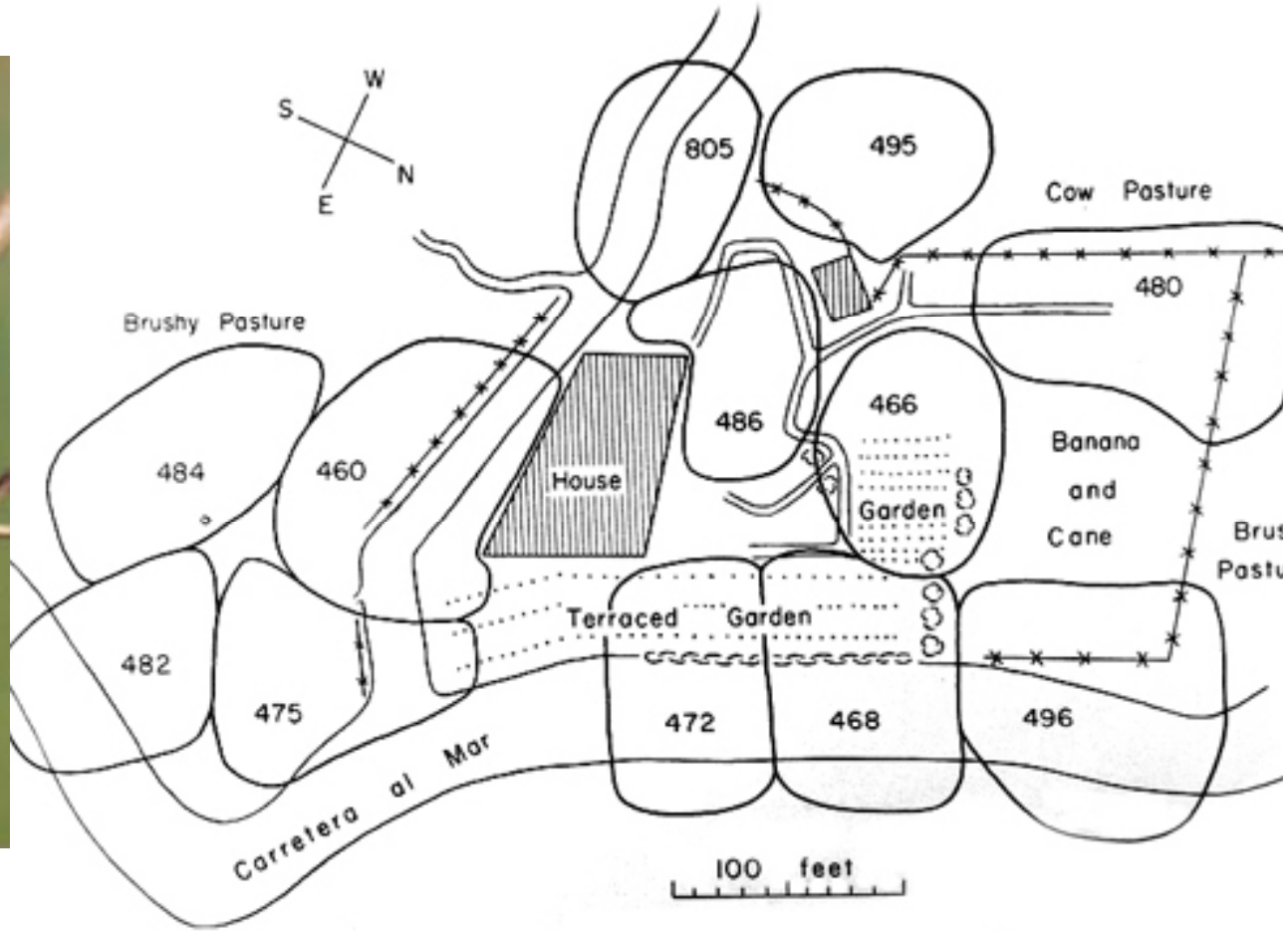
(2) Retaliatory: always responds to a partner that is cheating.

(3) Forgiving: only remembers one move back in time.

Examples in animals?

Tit for tat Example #1: Neighboring males defend territories

Two neighboring territorial animals become less aggressive toward one another once territorial borders are well-established. As territory owners become accustomed to their neighbors, they expend less time and energy on defensive behaviors directed toward one another.



	Neighbor		
Focal Male		Cooperation	Defection
	Cooperation	**Cooperation**- save energy by avoiding confrontations	**Sucker's payoff :** looses territorial resources or females
	Defection	**Temptation** to gains resources and females and keeps its own	**Mutual defection** - - come up even

The payoff matrix:

Temptation> Cooperation > Mutual Defection > Sucker's Payoff

Tit for tat strategy example #2

Food sharing in blood-sucking vampire bats

Female bats regurgitate blood meals to others that failed to obtain food

Food sharing "tit for tat" in blood-sucking vampire bats

1. Colonial bats that can recognize one another are more likely to give blood to those that have donated blood to them in the past (reciprocate)

2. Blood sharing is a huge benefit for recipient but not a big cost for donor.

Prisoner's dilemma and Tit for tat strategy

- In a one-time game, you should defect because the average payoff is greater.
- If the game is to be repeated many times, it is in both player's long-term interest to cooperate.
- Tit-for-tat is an evolutionarily stable strategy, or solution, to a repeated Prisoner's Dilemma game. The rule is: cooperate on the first play and then do what your opponent did in the last play.

Decision making “tit for tat” in humans

		Player B	
		Cooperate	Defect
Player A	Cooperate	Reward for mutual cooperation	Maximum punishment
	Defect	Maximum reward	Punishment for Mutual defection

Playing “Tit for tat” in the fMRI (monitoring brain activity)

1. Most emotionally rewarding payoff is “both cooper
(induce highest neural activity in brain’s reward area
even though the most monetary reward is to “cheat

2. Subjects derived pleasure from punishing cheaters
(induce high neural activity in reward area when
punish the cheater).

3. When subjects mutually trust, oxytocin increases.

Types of social interactions

1. Mutualism (cooperation)
2. Reciprocity
3. Altruism
4. Selfish behavior
5. Spiteful behavior

3. Altruism

Helper (lose); recipient (gain)

Donor (helper) really does permanently lose opportunities to reproduce
as a result of helping another produce more surviving offspring.

--reduce individual's reproductive success

The Conundrum of Altruism

- **Selfish and mutualistic acts increase the fitness of the actor. It is clear that these behaviors will be selected for by natural selection, because those who act selfishly or mutualisticly derive a direct/immediate benefit from their action.**

- **Altruism is a problem to explain because by definition it decreases the fitness of the individual performing the behavior while increasing the fitness of a competitor (the recipient) and therefore reduces the contribution of the genes that underpin that behavior to the next generation.**

How can altruism ever evolve?

1. Group selection (controversial)?

2. Indirect selection (Kin selection)
   (W. D. Hamilton: kinship theory)

Halmilton's kinship theory - inclusive fitness -

* **Inclusive fitness**: an individual's total fitness is based on the number of its own offspring and the contribution it makes to the reproductive success of its genetic relatives.

* include both direct fitness (your own offspring) and indirect fitness (your sib's offspring, your grandchildren).

How to calculate indirect fitness?

Two siblings are related to one another by **r=0.5**

Sibling #1 has gene A, 50% (0-100%) chance she received gene A from her mom.

Sibling #2 has gene A, 50% (0-100%) chance she received gene A from her mom.

There is 25% chance (50%x50%) that the siblings share gene A through their mother.

There is 25% chance that the siblings share gene A through their father.

The chance that the siblings share gene A through either their mother or father: 25% + 25% =50%

The chance that the siblings share gene X through the parents =50% r (**relatedness)** =0.5

Quiz:

The genetic relatedness between cousins: r = ?

The genetic relatedness between grandparents and grandchild: r = ?

Hamilton's Kin selection:

Hamilton's (1964) theory of kin selection predicts that altruistic behaviors will be favored by selection if the costs of performing the behavior are less than the benefits to the receiver discounted by the relatedness between actor and recipient.

What would you do ? If he/she is a stranger, your cousin, sibling, or your parent? Will you rescue the person dependin on your relatedness?

Hamilton's rule:

$$c < rb$$

c = cost of the helper
b = benefit to the recipient
r = relatedness between helper and recipient

Calculate inclusive fitness

Direct fitness: N1 survive because of parental care (individual produces offspring)

Indirect fitness: N2 survive because of help (individual helps relatives)

Direct fitness: N1 x r

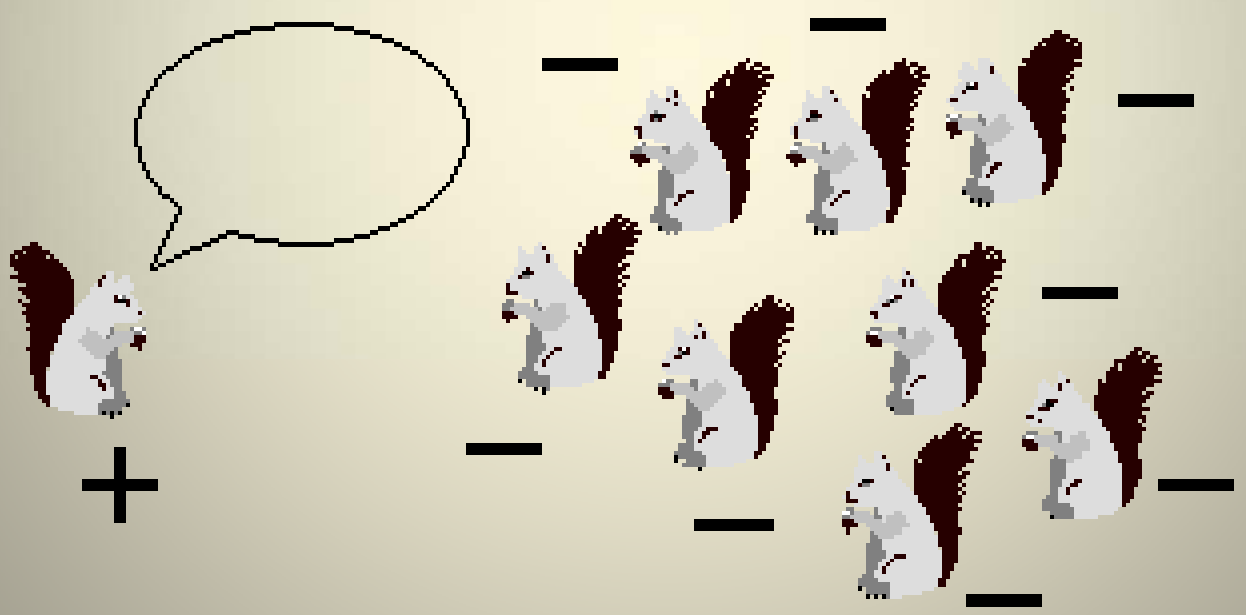
Indirect fitness: N2 x r

Why do ground squirrels produce alarm calls, sometimes?

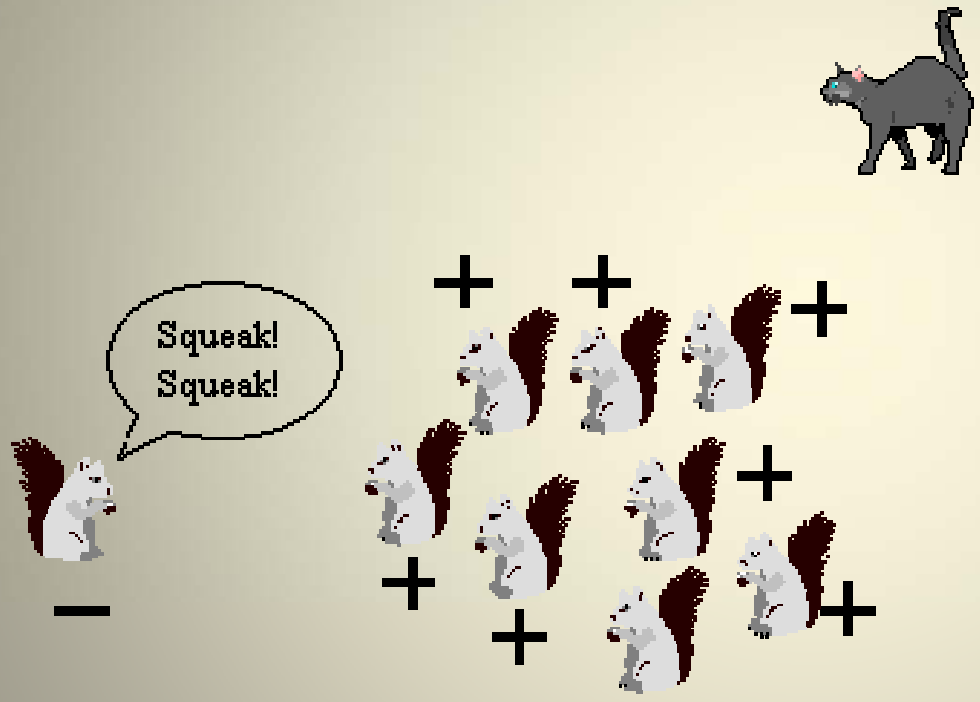
Altruism and Warning Calls

Gives a warning call
(ACTS ALTRUISTICALLY)

Doesn’t give a call (ACT SELFISHLY)



Giving the warning call and accounting for kin selection where the cost of giving the call is .3 and the benefit .1 to each of the others and the actor is the sister of the others (r = .5)



c = .3

b = .1 x 8 = .8

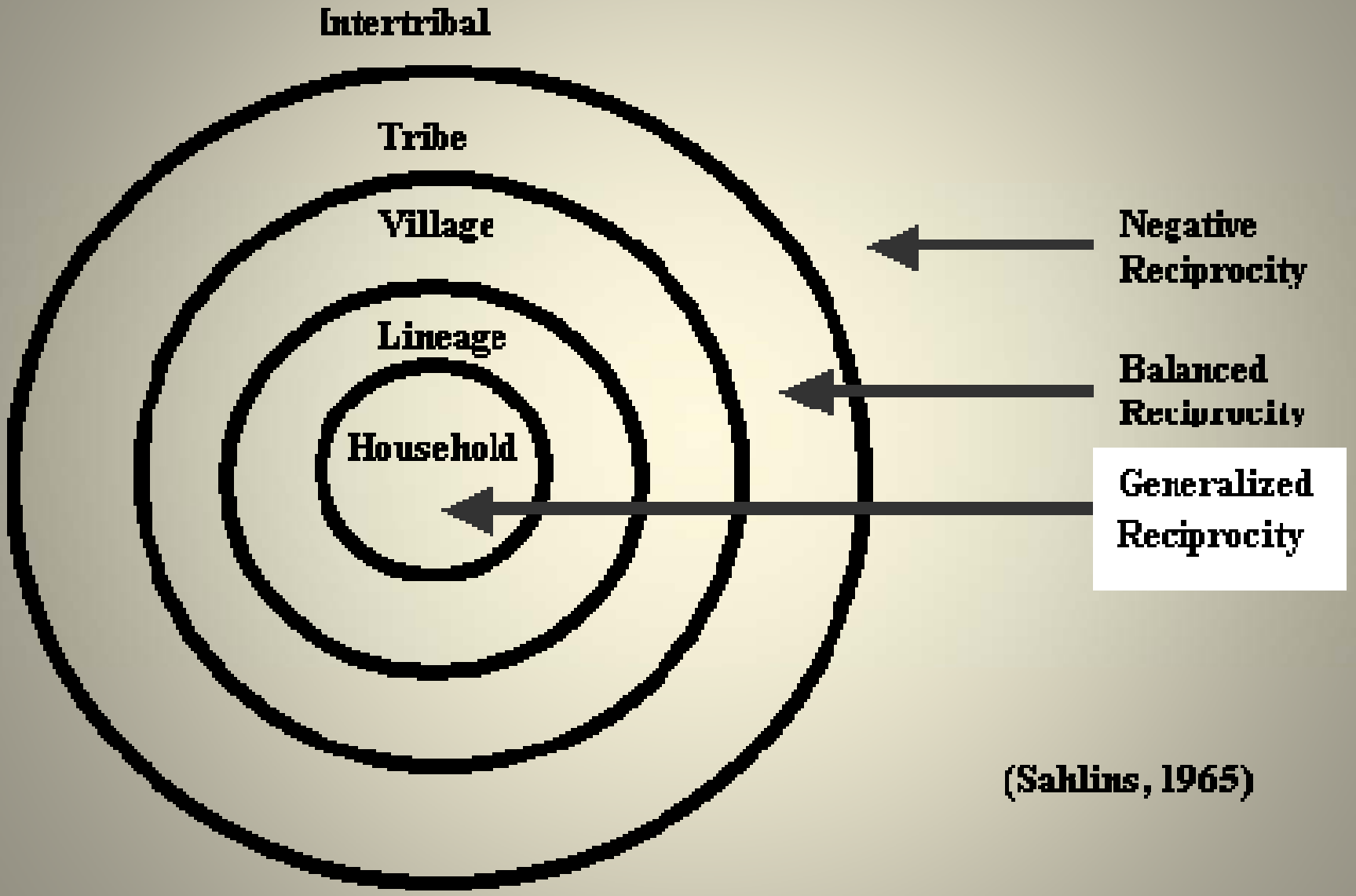
r = .5

rb = .5 x .8 = .4

Give the warning call because c<rb (.3 < .4)

- **Kin selection is a powerful motivation for cooperation in social interactions.**
- **Kinship is an important principle for the organization social structures**
- **In humans, tribal and band societies kinship is the primary principle around which groups form and is primary in defining the relationships between groups.**

Spheres of Interaction and Exchange



(Sahlins, 1965)

Examples of altruistic behavior (kin-selection) in animals?

1. Ground squirrel produces alarm calls to warn neighboring relatives.

2. Pied Kingfishers help their parents to care for the siblings

Altruism in Pied kingfisher

Altruism in Pied kingfisher

1. Nest colonially → social
2. Some young males are unable to find a mate
   become primary helper,
   help their mom and nestlings (siblings)
3. Some males become secondary helper,
   help non-relatives
4. Some males sit out and wait for next year-- delayer
5. Many males find a mate next year and have
   their offspring.

What strategy is the best (max benefit/ cost)?
Primary, secondary helper ? Or delayer?

Altruism in Pied kingfisher

The benefits and costs of helping behavior what behavioral strategy is the best?

	Young r f1 First year	O r s m f2 Second year (paired)
Primary helper	1.8 x 0.32 = 0.58	2.5 x 0.50 x 0.54 x 0.60 = 0.41
Secondary helper	1.3 x 0.00 = 0.00	2.5 x 0.50 x 0.74 x 0.91 = 0.84
Delayer	0.0 x 0.00 = 0.00	2.5 x 0.50 x 0.70 x 0.33 = 0.29

Young= number of young nestlings they help;
r= relatedness; **f1**= fitness in year1;
O= offspring; **s** = p of survival to next year;
m= p of finding a mate in the second year

Altruism in Pied kingfisher

Why helping non-relatives (2nd helper)?

Hypothesis: Ecological constraints:

--availability of limited territory

--availability of females

Helper can better access the resources (territory, females, food) next year.

How to test this hypothesis?

Summary

Evolution of Helper's altruism

1. Kin selection
   Inclusive fitness $C < *b x r$

2. Ecological constraints.

   (helpers to stay or to disperse depending on resource availability)

Benefit or cost?

Outcome	Actor	Recipient
Mutualism	+	+
Reciprocity	+ (delay)	+
Altruism	- (direct)	+
Selfish	+	-
Spiteful	-	-

The evolution of eusocial behavior

What is eusocial behavior?

A form of social organization characterized by:

1. Adults live in a group.
2. Cooperative care of juveniles
3. Labor division
4. Overlap in generations

What species are eusocial?

Arthropoda				
	Class: Insecta			
		Orders:		
		Isoptera		All eusocial, many advanced
		Hemiptera		~50 sp eusocial
		Thysanoptera		~6 sp eusocial
		Coleoptera		1 species "Ambrosia beetle"
		Hymenoptera		
			Ants	All species (except a few highly derived species) ~14000
			Bees	Only 300-400 of ~ 4000 sp are eusocial
			Wasps	Most are not social, ~900 species are eusocial
	Subphylum: Crustaceae			
		Snapping shrimp		*Synalpheus*
Chordata				
	Class: Mammalia			10's of primitively eusocial species
		Family: Bathyergidae (African mole rats)		2 advanced eusocial species: naked mole rat (*Heterocephalus glaber*), Damaraland mole rat (*Cryptomys damarensis*)

Honey bee

1. Adults live in a group.
2. Cooperative care of juveniles (even not their own)
3. Labor division (workers are sterile)
4. Overlap in generations

Many eusocial species:

Reproductive division of labor evolves from sterile castes which often have helping behavior (female workers).

Why they sacrifice their own reproductive success to help others (altruism)?

How did Eusociality evolve?

Darwin (1859) commented on the challenge of understanding eusociality as "one special difficulty, which at first appeared to me insuperable, and actually fatal to the whole theory…"

-- how can individuals benefit without producing offspring

Hamilton's rule: altruism can evolve if:

$$*C < *b \times r_b$$

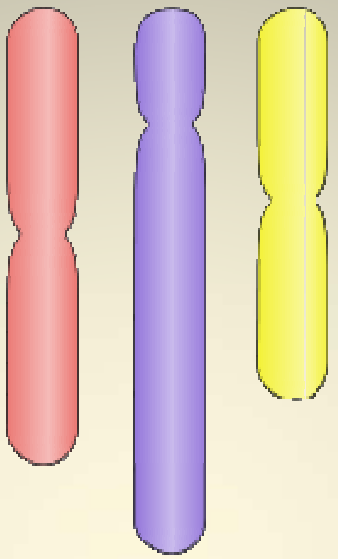
If the relatedness of the altruist to the relatives it helps (r_b) is particularly high, then indirect fitness would be increased.

True in many eusocial insects !

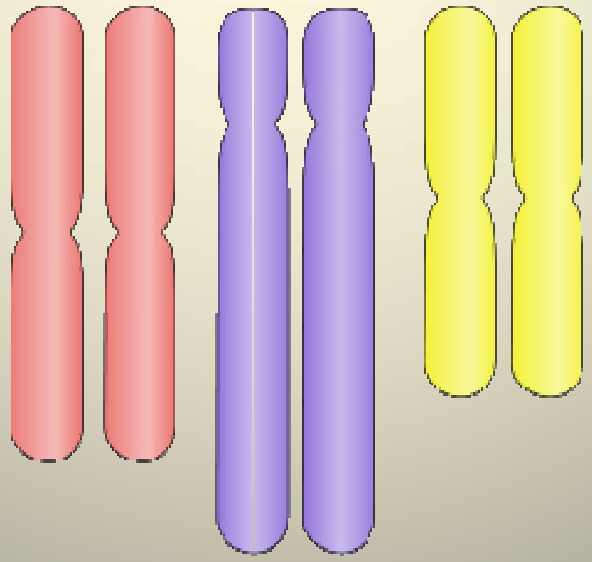
How did Eusociality evolve? --increase inclusive fitness

1. Kin selection by haplodiploid, r ↑
2. Kin selection by inbreeding, r ↑
3. Ecological (resource) constrains
4. Multi-level selection (including group selection)

Haploid (N)



Diploid (2N)



In bees, ants and wasps (haploidiploid species)

Males come from unfertilized eggs – haploid (one set of chromosomes) ; sperms of each male are identical

Females come from fertilized eggs – diploid (two set of chromosomes) - eggs of each female are 50% identical

A female mates with a male: all her diploid daughter will carry the same set of paternal genes, but carry 50% of maternal genes

Therefore, **haploidiploid sisters** will share 75% of genes

Helping sisters indeed increase indirect fitness

Sisters help sisters

	Mother	Sister	Daughter	Father	Brother	Son
Haplodiploid						
female	0.5	0.75	0.5	0.5	0.25	0.5
male	1	0.5	1	0	0.5	0.25
Diploid						
female	0.5	0.5	0.5	0.5	0.5	0.5
male	0.5	0.5	0.5	0.5	0.5	0.5

haploidiploid sisters share 75% of genes
diploid sisters share 50% of genes

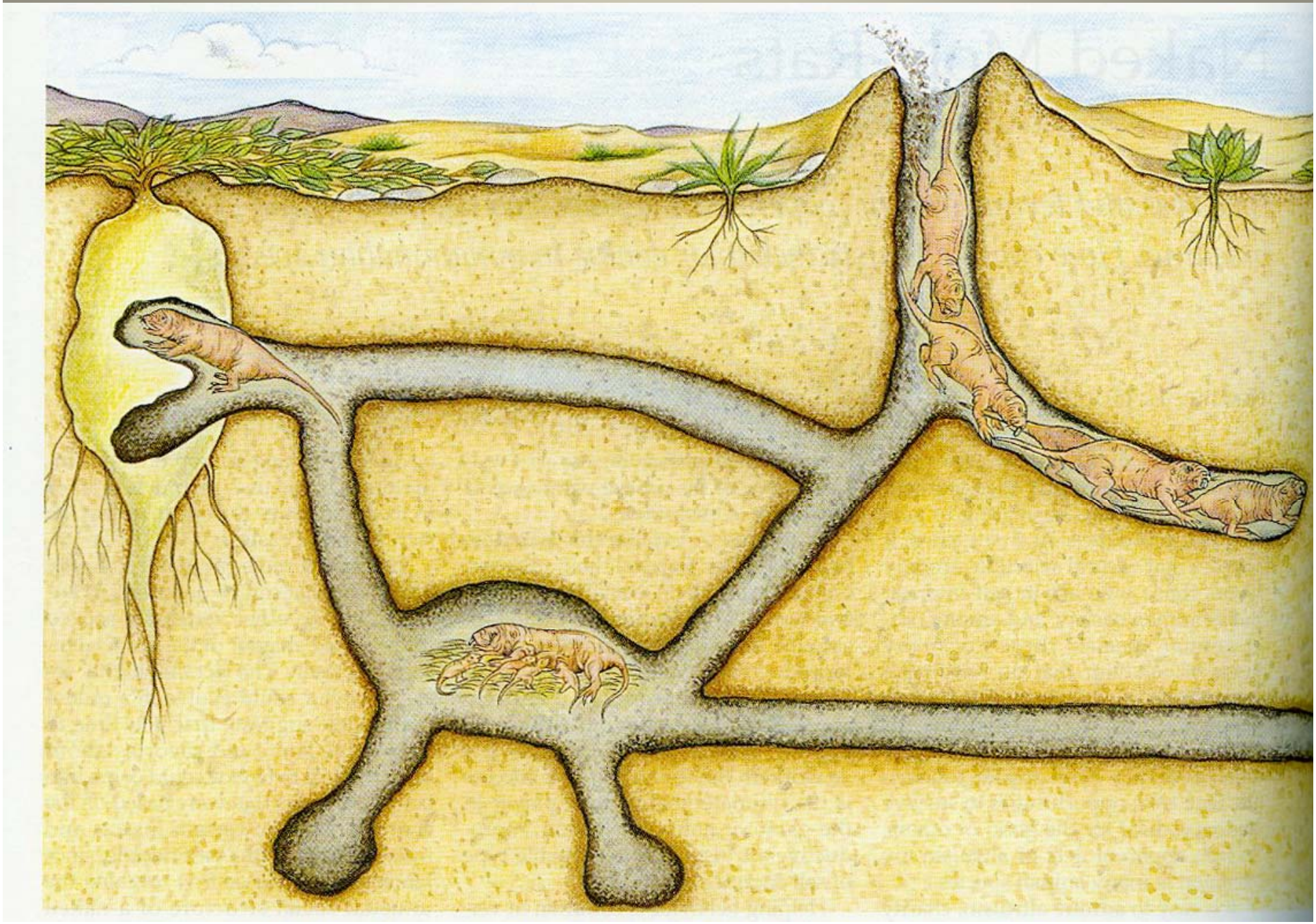
$$*C < *b \times r_b$$

Eusocial females would be expected to prefer to help their mothers raise their sisters, increasing their indirect fitness, rather than concentrating on increasing their direct fitness by raising their own offspring.

How did Eusociality evolve?

1. Kin selection by haplodiploid, r ↑
2. Kin selection by inbreeding, r ↑
3. Ecological (resource) constrains
4. Multi-level selection

Example of eusocial animal: Termite: diploid



Naked mole-rats: eusocial mammals

1. Diploid animals

2. One queen with a few kings in a colony (70-80 individuals per colony)

3. Other females as sterile, altruistic workers (labor division); cooperative care of juveniles

4. A lot of inbreeding (therefore siblings are more close related than their own offspring)

5. Why this species evolves eusocial behavior?

Naked mole-rats: eusocial mammals

Due to intense inbreeding, the siblings are more related to each other, even more related to their parents.

It is thus beneficial for females to help their parents to take care of the siblings.

How did Eusociality evolve?

1. Kin selection by haplodiploid, r ↑
2. Kin selection by inbreeding, r ↑
3. Ecological (resource) constrains
4. Multi-level selection


Live in harsh ecological environment with limited,
patchy food resources– favor the evolution of

How did Eusociality evolve?

1. Kin selection by haplodiploid, r ↑
2. Kin selection by inbreeding, r ↑
3. Ecological (resource) constrains
4. Multi-level selection

Multilevel selection

Natural selection works on the level of

1) Genes
2) Individuals
3) Groups

Sports such as bicycle racing illustrate some of the same conflicts between group and individual interests seen in biological evolution. A small group of cyclists can sustain a higher speed if they coordinate their efforts, with each rider taking a turn at the front of the group, where wind resistance is greatest, and then resting in the wake of the others. Each rider is competing as an individual and so has an incentive to conserve energy until the last moments of the race.. Analogous situations arise in evolutionary biology, where individuals compete within a group while groups compete against one another.

Social interaction among species beneficial for both species?

Not in the cuckoos

Social interactions among species (honeyguides and humans)

Mutualistic for both species